

Changes in assemblages of native and alien plants in perennial plantations: prairie species stabilize the community composition

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Abstract

Ornamental plantations are characteristic of a wide range of man-made habitats such as gardens, parks or urban spaces. Nowadays, low-maintenance perennial beds are becoming popular in horticulture and urban planning. Due to low levels of management and good records of initial plantation, perennial beds are suitable for studying vegetation processes such as competition amongst garden ornamentals and succession. We studied perennial flowerbeds in the Czech Republic that had a known initial composition at the time of establishment in 2006–2010 and we compared this with their state in 2016. We aimed to assess (i) how planted ornamental assemblages changed during 10 years of succession, and (ii) whether initial assemblage composition determined the pattern of change. We observed a decrease in biodiversity from initial plantation to the recent state across all flowerbeds in the experimental garden. In terms of diversity and stability, species-rich assemblages, mostly composed of taxa native to prairies, were the most stable. The most successful taxa (i.e. reaching high abundances with good persistence) originated from North American and Mediterranean regions.

Keywords

Artificial habitats, diversity, flowerbeds, horticulture, long-term monitoring, plant assemblage, species origin

Introduction

Ornamental horticulture is associated with humans since the dawn of agriculture (Relf 1992; Zhou 1995; van Kleunen et al. 2018). Ornamental plants comprise any plant that is charismatic regardless of their origin (Jarić et al. 2020). Many such plants were moved around the globe to closely resemble home to the colonists or to increase the diversity of the garden flora (Wyman 1968; Reichard and White 2001; Daehler 2008). Ornamental plantations serve as a significant source of aliens, particularly naturalized and invasive plants worldwide (Reichard and White 2001; Ruiz and Carlton 2003; Dehnen-Schmutz et al. 2007; Hulme et al. 2008, 2018; Pergl et al. 2016). Frequently planted ornamental alien species are more likely to naturalize outside cultivation than less frequently planted species (Mulvaney 2001). Thus, one of the reasons why species introduced by the horticultural pathway represent more than 49% of the current global naturalized flora (van Kleunen et al. 2018) is due to intensive and long-lasting propagule pressure (Dehnen-Schmutz and Touza 2008; Pyšek et al. 2015). In some European countries this proportion is even higher – for instance, more than 58% of aliens in the British Isles are classified as garden escapes (Clement and Foster 1994), and in the Czech Republic 74% of intentionally introduced alien flora comprise ornamentals (Pyšek et al. 2002). Furthermore, the pool of potentially invasive taxa is continually enhanced through breeding and deliberate hybridization, processes that enhance the effects of colonization pressure (Ellstrand and Schierenbeck 2000; Mack 2000; Lockwood et al. 2009). Selection and breeding not only increase attractiveness of ornamentals but make them better adapted to local conditions, contributing thus to the higher risk of naturalization (Anderson et al. 2006). The probability of naturalization success is influenced also by the geographic range of species. A large native area makes species better preadapted to the conditions in the invaded range (Rejmánek 1996; Sax and Brown 2000; Pyšek et al. 2009), and it has also been shown that aliens from some regions are more successful than those from others, depending on environmental match between the donor and the invaded area (Castro et al. 2005; Aronson et al. 2007). Also, some grown taxa are confined to habitats such as steppe or prairie in their native range and establish better in corresponding habitats following introduction (Köppler et al. 2014; Hejda et al. 2009, 2015).

Ornamental planting has traditionally been a topic of interest for garden designers and landscape architects (Jongman 2002; Köppler et al. 2014). However, ecologists (e.g. Vilà 2003; Pergl et al. 2016; Haeuser et al. 2018; Kutlvař et al. 2019) and regional botanists (Hill et al. 2005; Pokorná et al. 2018) are well aware of the potential to use ornamental floras for studies in invasion ecology (Guo et al. 2019) as they share the interest with garden designers to identify species that are easy to grow and naturalize (van Kleunen et al. 2018). Requirements of land managers and gardeners for low management have been met recently by using so-called mixed perennial beds (Messer 2008; Baroš and Martinek 2011, 2018; Kutlvař et al. 2019). Such flowerbeds usually include native and alien taxa (i.e. species, subspecies, varieties, cultivars and hybrids) and are based on the autoregulation principle. This principle is inspired by

natural systems and processes and does not require as much maintenance as commonly used plantations. Flowerbeds established in this way (i) need not be planted repeatedly because they persist through self-seeding and/or vegetative reproduction; (ii) do not require regular watering as they are composed of drought-tolerant taxa; and (iii) their stability over time is safeguarded by using taxa with various functional roles, such as covering, grouping, or complementary taxa (Baroš and Martinek 2011).

The flowerbeds are usually composed of both native and alien taxa. This provides an opportunity to compare the performance of alien vs. native species in succession, to find out how both groups perform relative to each other. The differences in behaviour of native, alien non-invasive and alien invasive species have been used to search for the determinants of invasion success and many studies show the differences between natives and aliens in their ability to spread and other traits (e.g. Daehler 2003; Pyšek and Jarošík 2005; van Kleunen et al. 2010; Chrobok et al. 2011; Čuda et al. 2015; Maurel et al. 2016). Moreover, the impact of dominant species is the main focus of nature conservation, policy makers and managers and therefore it is important to identify whether the management, namely prevention, should be focused only on aliens, as is often done, or also on some native species.

In general, many ornamental plants are sterile hybrids. Such reproduction strategy is, however, not suitable for permanent beds as in order to persist, species should be capable of sexual or vegetative reproduction. The different role that sexually and vegetatively reproducing species play in succession may then lead to the formation of different assemblages. However, many species share both reproduction systems, generative and vegetative, in various proportions (Sailer et al. 2020). Species producing many viable seeds and at the same time able to reproduce vegetatively are more successful in persisting in ornamental beds than those lacking such ability (Kutlvašr et al. 2019). In addition, many taxa, particularly hybrid ones, compensate for their sterility by robust vegetative reproduction.

Processes shaping the stability of artificial assemblages of ornamental plants are also relevant for studies assessing diversity-stability relationships. Natural, species-rich communities are relatively stable (in terms of species composition and abundances) compared to species-poor communities that show high levels of fluctuations (McNaughton 1978). Such conclusions are based on observations of natural communities and only a few experimental studies include enough species which can be used to infer generalizations about resilience and succession (Rydgren et al. 2004; Ma et al. 2019). Therefore, there is a lack of knowledge on the development and succession of species-rich artificial assemblages as well as natural communities. Understanding the course of succession in such species-rich assemblages could help to understand the ability of different species to naturalize, because aliens escaping from cultivation in perennial beds need to cope with ornamental assemblages developing over time.

Despite the lack of suitable experimental designs, plantations are a good model system for studying succession by following ornamental assemblages with known initial composition over time. An advantage of using such systems is that initial composition as well as management of perennial plantations is usually well documented (Baroš 2011).

Moreover, assemblages of perennial plantations usually include a broader spectrum and a larger number of taxa compared to well-designed ecological experiments in mesocosms that were used to study the diversity-stability relationship (Boyle and Fairchild 1997; Emery and Gross 2007).

In our previous research, we studied the fate of individual species and their traits in perennial plantations (Kutlvař et al. 2019). Here, we assess whole assemblages in perennial beds and their development over time, analogous to vegetation succession. We ask the following questions: (i) How has the composition of planted ornamental assemblages changed since flowerbed establishment? (ii) Is there a relationship between the rate of change in species composition of ornamental assemblages and the diversity of planted taxa? (iii) Are there any differences in how native, alien and hybrid taxa change their dominance? and (iv) Is the geographic origin of the planted taxa important for the outcome of succession?

Methods

Study site and vegetation sampling

This study was carried out on 19 perennial flowerbeds (FB) that are growing in the Dendrological Garden of the Silva Tarouca Research Institute of Landscape and Ornamental Gardening in Průhonice, Czech Republic (50.01°N, 14.56°E; see details in Kutlvař et al. 2019). The climate in the Czech Republic is transitional between temperate oceanic in the west and temperate continental in the east (Rivas-Martínez et al. 2004). The climate in Průhonice is dry and warm with a mean annual temperature of 8–9.5 °C and an annual precipitation of 400–600 mm (Tolasz et al. 2007).

The FB were established in 2006–2010. Their sizes varied between ~75–125 m². Each FB was separated by a belt of lawn that was at least 3 m wide. Various ornamental assemblages commonly used in urban and suburban landscapes were planted in each FB. The FB were composed of taxa originating mainly from North America, Mediterranean and Eurasia (see supplementary material in Kutlvař et al. 2019 for a list of planted taxa); some FB are grown in mixtures with native Czech taxa. To achieve a high level of autoregulation, the assemblages were established for horticultural purposes without a proper statistical design. Moreover, the taxa selected for initial planting (not sowing) were chosen to minimize their maintenance. This included steppe, prairie and drought-tolerant taxa that did not demand any watering (Baroš and Martinek 2011). The beds were mulched immediately after planting and covered with a 50–70 mm deep layer of gravel (Baroš 2011, 2014). Dry biomass was removed from FB at the end of winter and weedy taxa (e.g. *Taraxacum* sect. *Taraxacum* spp. and *Bellis perrenis*) were pulled out during the vegetation season. Weeding, in particular, plays a major role because it creates gaps in compact vegetation cover, providing open spaces for colonization by planted species and other plants (see Kutlvař et al. 2019).

For each FB, we compared the initial ornamental assemblages at the time of planting and recent assemblages as recorded in June to September 2016. Taxa that colonized the FB from the surroundings were included as a recent recording. The initial taxonomic composition was derived from the number of planted individuals that served as a basis for calculating their percentage. For the recent composition, we recorded the cover of individual taxa by using the Braun-Blanquet abundance and dominance scale (Braun-Blanquet 1921, 1951). Each FB was divided into three plots (i.e. replicates) of $\sim 25 \text{ m}^2$, except FB 6 and 12 that were divided into five replicates due to their larger size. Thus, we sampled 61 plots in total. All vascular plants including cultivars, hybrids and varieties (these groups are further collectively referred to as ‘cultivars’) were recorded in each plot and assigned a cover value, except for early spring geophytes.

Data analyses

For each plot and time (i.e. initial vs recent), we calculated the Shannon-Wiener index of diversity (H' index) and the number of taxa (Lepš 2005). For each taxon occurring in the initial and/or recent assemblage, we recorded its status (i.e. alien/native/cultivar), vegetative/generative reproduction (see Kutlvašr et al. 2019 for assessment of reproduction), and for aliens we also recorded their geographic origin classified into eight regions (i.e. Africa, Asia, Australia, Europe, Mediterranean, North America, Central and South America, and cosmopolitan). The origin of cultivars was not considered, this group included both native and alien taxa and was treated separately in analyses. Taxa native to more than one region were assigned to all regions in which they occur. Data on origin was obtained from the Plants of the World database (<http://powo.science.kew.org/>) and manually checked in the respective floras. The nomenclature was unified according to The Plant List (<http://www.theplantlist.org/>).

Differences among initial Shannon-Wiener index of individual FB were analyzed using an ANOVA with a post-hoc test of differences using Tukey’s HSD. To analyze the change in assemblages over time, we calculated the Euclidean distance between the initial and recent assemblage in multidimensional ordination space. For calculation of the positions, we used canonical correspondent analysis (CCA; ter Braak and Šmilauer 1998), taking into account the cover of individual taxa (species data). Species data were logarithmically transformed ($Y' = 1 + Y$). To calculate the distance between the initial and recent assemblage within the plot, the first four CCA axes were used. The distances were then averaged for each FB (further referred to as average change). The significance of the time of establishment was tested using the Monte Carlo permutation test, a total of 499 permutations. The FB were set as a grouping factor and the analyses were performed in CANOCO 5 (ter Braak and Šmilauer 2012).

To test for similarities between initial and recent taxonomic composition of assemblages, we performed hierarchical cluster analysis with Ward’s minimum variance clustering, a method based on the linear model criterion of least squares (Crawley 2007). First, we calculated a matrix of Euclidean distances of square-transformed and

normalized abundance values using the Vegan package (Oksanen 2015). The optimal number of clusters was determined according to silhouette widths (package Cluster; Maechler et al. 2018). We used tanglegram to compare initial and recent tree of hierarchical clustering (package Dendextend; Galili 2015). Following the cluster analysis, we used a one-sample t-test based on the average change in order to identify significant differences between two main clusters. This analysis was performed in R version 3.3.2 (R Development Core Team 2019).

Regression tree analysis was used to identify variables that were associated with average change of the ornamental assemblage. Regression trees were selected because they allow to visualize the interactions between the analyzed factors, deal efficiently with combinations of multicollinear and categorical and/or numeric explanatory variables, and possess the capacity to treat missing data (De'ath and Fabricius 2000). Explanatory variables were based on the initial state of FB; for this we used H' index, number of taxa, number of alien/native/cultivars, reproductive strategy and origin. The trees were constructed using binary recursive partitioning, with the default Gini index impurity measure used as the splitting index, in CART v. 8.0 (Breiman et al. 1984; Steinberg and Colla 1995). To find an optimal tree, a sequence of nested trees of decreasing size, each being the best of all trees of its size, was grown, and their resubstituting relative errors, corresponding to residual sums of squares, were estimated. Ten-fold cross-validation was used to obtain estimates of cross-validated relative errors of these trees. Following De'ath and Fabricius (2000), a series of 50 cross-validations were run, and the most likely (i.e. modal) single minimum cost tree was chosen for description.

Results

Trends in ornamental compositions

In total, there were 272 planted taxa across 19 flowerbeds. An average number of taxa per FB was 24 (min. 12; max. 35) and 27 (min. 11; max. 36) for initial and recent assemblages, respectively. In the recent inventory (i.e. 2016), we found 266 taxa but 34 of them were classified as new taxa that naturally spread to the FB. Two taxa from this naturally spreading group are alien in the Czech Republic (i.e. *Conyza canadensis* and *Solidago canadensis*) and 32 are native. On the other hand, 40 (15%) planted taxa disappeared over time. Among the initially planted taxa (i.e. 2006–2010), there were 109 aliens (41%), 39 natives (14%) and 123 cultivars (45%) compared to 85 aliens (32%), 76 natives (29 %) and 95 cultivars (36%) in the recent assemblages (Fig. 1; eight taxa were not assigned status due to insufficient determination).

The Shannon-Wiener diversity decreased between the initial plantations ($H' = 2.65 \pm 0.37$) and the recent inventory ($H' = 2.39 \pm 0.36$) and this trend was apparent

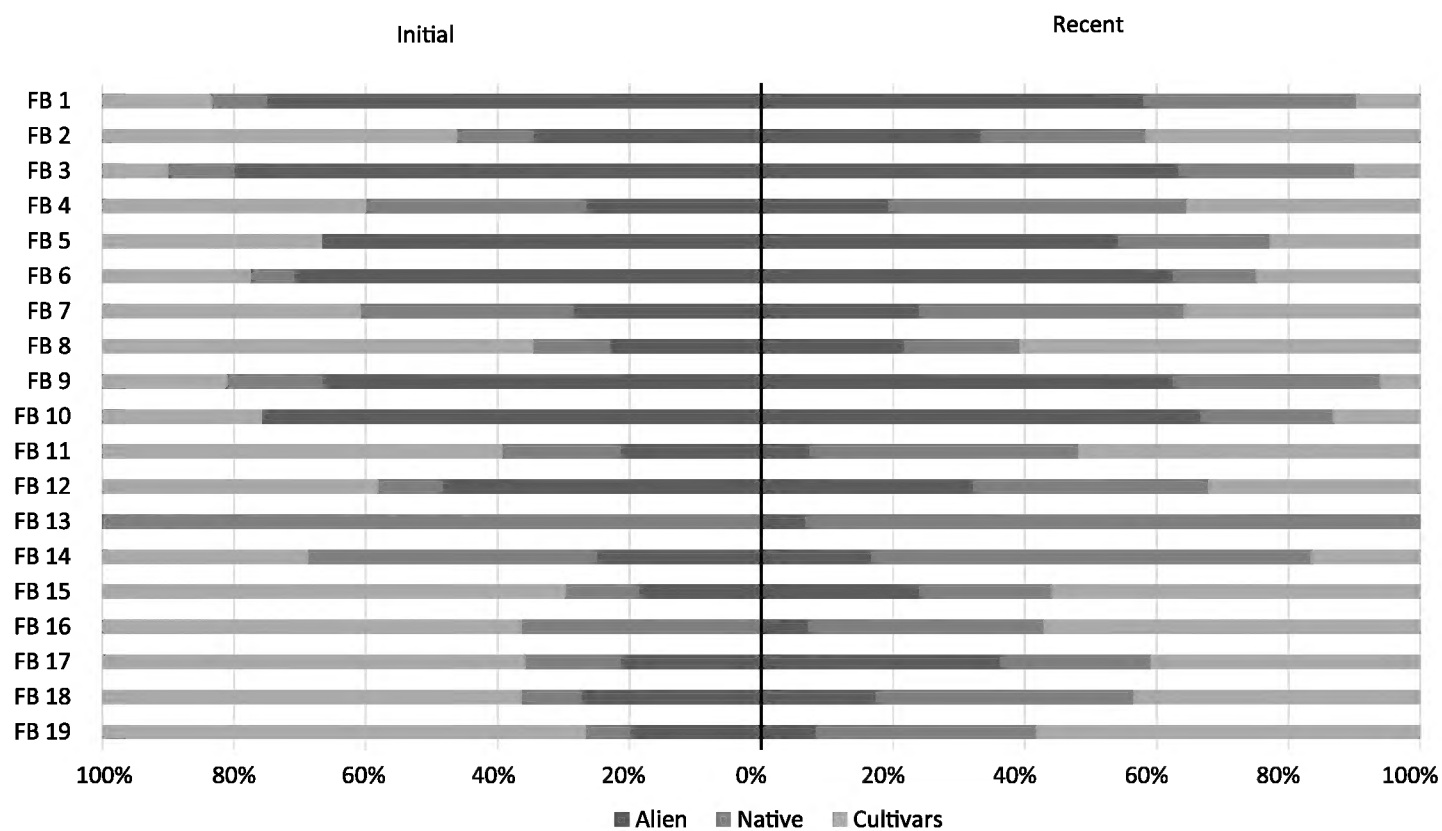


Figure 1. Percentage of taxa present in each flowerbed separated according to initial vs recent ornamental assemblages. In addition, the colored bars are indicative of taxa classified according to their status (i.e. alien; native; cultivars) in the Czech Republic. Some FB (no. 13, 16) were established with exclusively native taxa or their varieties. In the recent assemblages all FB harboured alien taxa.

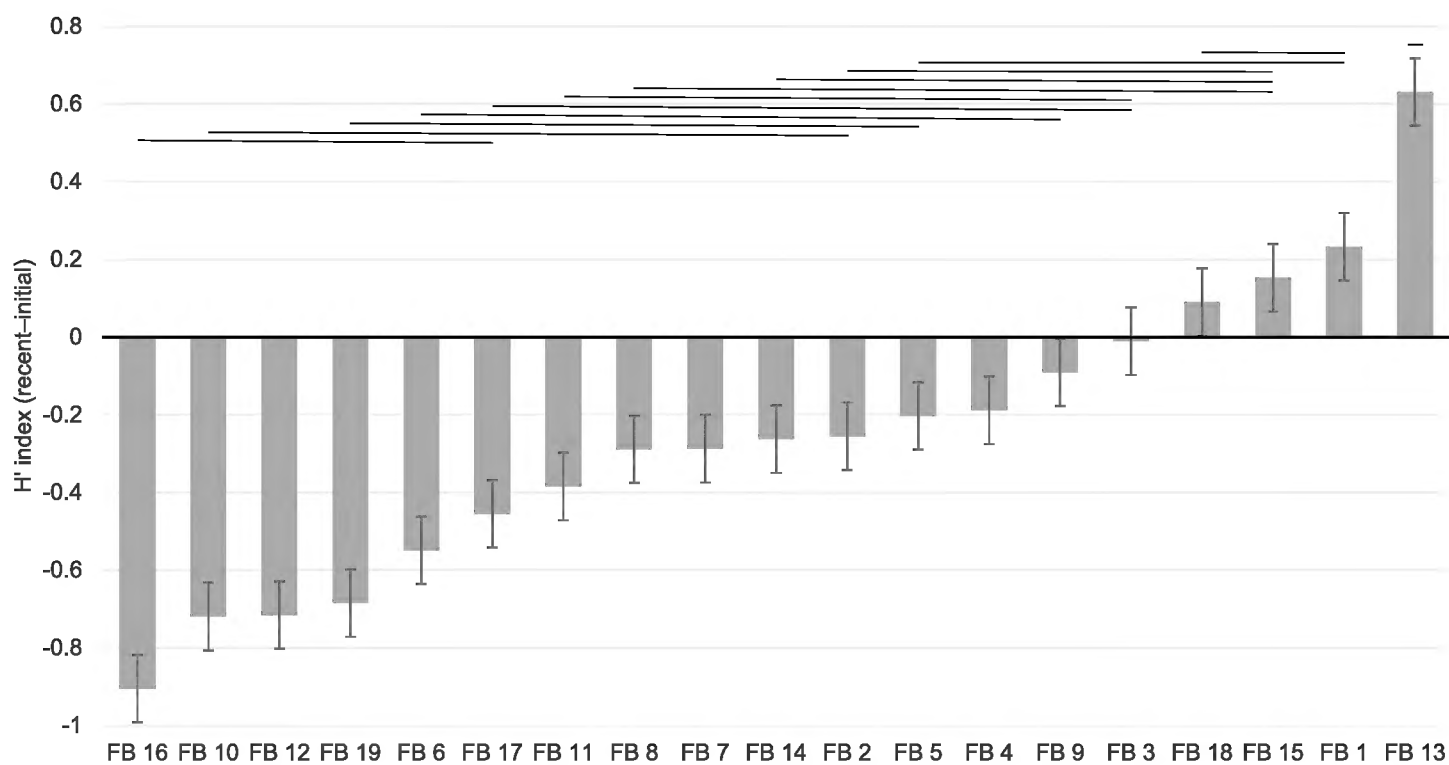


Figure 2. Bar plot depicting changes in the Shannon-Wiener diversity index (i.e. H' ; recent minus initial). Negative values show a decrease in diversity while positive values represent an increase in diversity over the study period. Segment lines show the standard error. Lines above the bars indicate significant differences amongst the flowerbeds at the level of $p < 0.05$ (Tukey's HSD test).

across the whole experimental garden ($F_{18,39} = 20.38, p < 0.001, n = 19$). There were only four FB (i.e. 1, 13, 15, 18, Fig. 2) in which biodiversity increased in comparison to 15 FB where biodiversity decreased (i.e. 2–12, 14, 16, 17, 19, Fig. 2). The correlation between the initial Shannon-Wiener index and the average change was not significant ($t_{17} = -0.79, p\text{-value} \geq 0.05$). Regarding the reproduction, we observed a 3% increase in taxa that are able to reproduce generatively and vegetatively. North American taxa were most successful, increasing their relative abundance on average by 13.3% across all FB. An increase in relative abundance was also recorded for the Mediterranean (5.7%) and cosmopolitan taxa (2.9%). On the other hand, taxa native to Central and South America (-23.2%), Asia (-7.7%), Australia (-6.4%) and Africa (-1.8%) decreased their relative abundance, and European taxa did not change in their abundance (Table 1, Fig. 3).

Table 1. Statistics showing the difference in abundance (i.e. recent vs initial state). Positive values indicate increase in abundance over time for the given group, negative values reflect decrease.

Measure	Africa	Asia	Australia	Europe	Mediterranean	North America	Central and South America	cosmopolitan
Σ recent-initial	-7.11	-146.02	-12.8	1.38	103.11	238.46	-208.85	31.84
Min	-15.42	-40.14	-9.67	-32.26	-26.32	-7.75	-49.21	-6.45
Max	12.25	21.77	0	32.24	41.63	63.33	2.3	31.81
Average	-1.78	-7.69	-6.4	0.07	5.73	13.25	-23.21	2.89

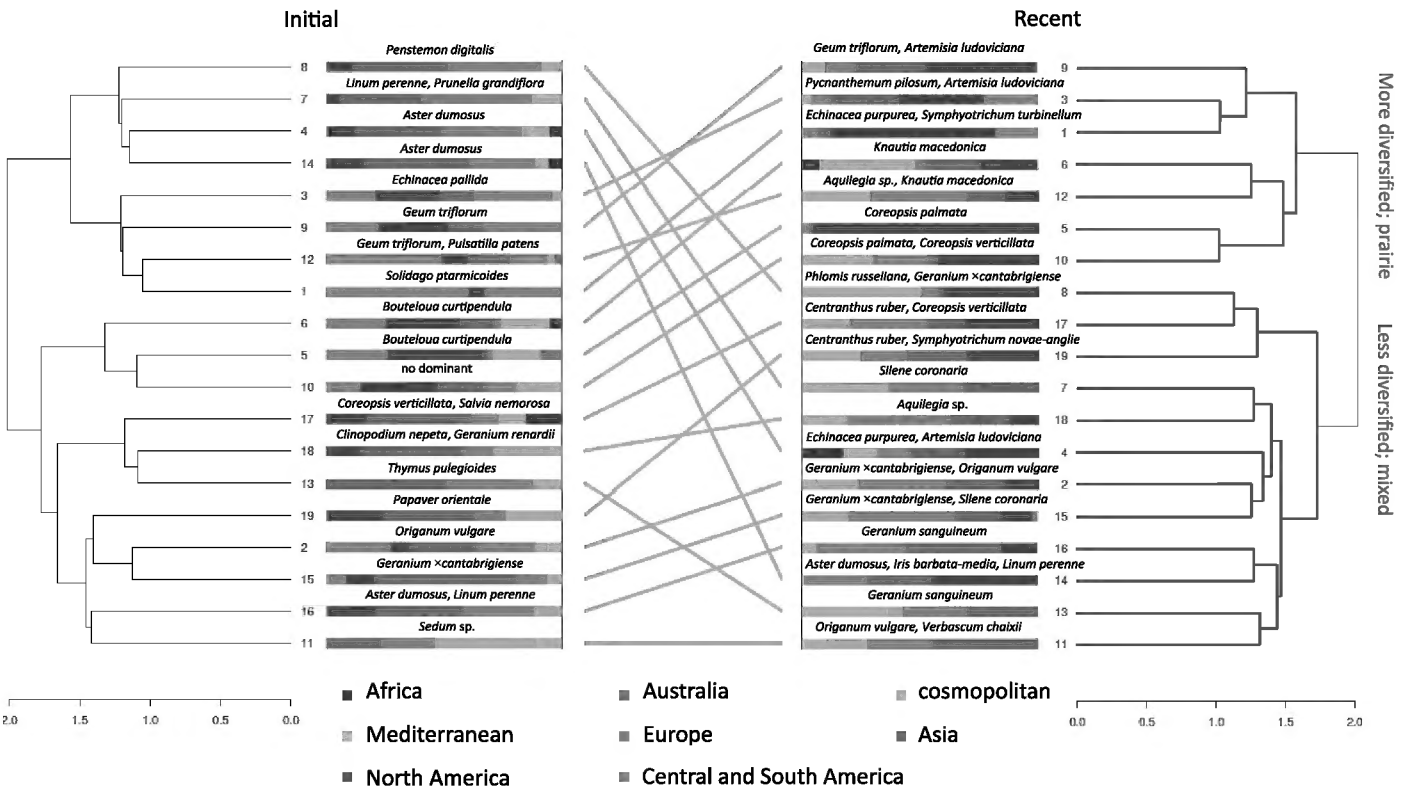


Figure 3. Cluster tree diagrams comparing initial and recent assemblages based on the average abundance. The cluster analysis distinguished two main clusters in the recent time assemblages. The bars represent the percentage contribution of taxa for a given origin. Only taxa that are highly abundant in the FB are shown by names. As the dominant taxa change over time, they are shown for both initial and recent stages.

Changes in ornamental assemblages

Over the period of ~10 years, there were shifts in abundance of ornamental assemblages across all studied FB (pseudo $F = 2.2$, $p = 0.002$). The average change for all assemblages in ordination space was 1.74. The highest change was found for FB 8 (4.67) and FB 17 (3.14), whereas FB 5 (0.55) and FB 16 (0.62) were most stable (Table 2). The results of the CCA analysis are summarized in the ordination diagram in Figure 4.

To identify the variables associated with the change of ornamental assemblages we used regression trees (Fig. 5). The tree based on average change of four ordination axes identified the initial number of taxa as the most important variable. The H' diversity index was also related to changes in assemblages. The smallest changes occurred in assemblages with more than 26 taxa (terminal node 3; resid. avg. 1.02), while species-poor assemblages were least stable (terminal node 1; resid. avg. 1.36). The lowest stability was recorded in assemblages with low species numbers and a high H' index (terminal node 2; resid. avg. 3.09).

Based on the clustering results of the recent inventory, we divided the FB in two clusters. The more diversified cluster included FB initially composed of largely prairie taxa and the less diversified cluster included FB typical of mixed taxa (Fig. 3). Testing the difference between the initial diversity (H') of FB belonging to these clusters revealed a significant difference ($t_{17} = -3.07$, $p = 0.007$), with the prairie cluster having a greater H' . In addition, we found a significant difference between the initial numbers of taxa ($t_{17} = -2.52$, $p = 0.002$), when the prairie FB were more diverse. On the other hand, our data did not show a difference between the average change of the two clusters ($t_{17} = 0.93$, $p = 0.36$).

Table 2. Average change of individual assemblages over the sampling period, based on the distance between initial (I) and recent (R) state in the CCA plot (see Methods for details on calculation), the Shannon-Wiener index (H') and numbers of taxa for different categories of origin and reproduction mode.

FB	Average change	H' (I)	H' (R)	All taxa (I)	All taxa (R)	All aliens (I)	All natives (I)	Cultivars (I)	Generative reproduction (I)	Vegetative reproduction (I)	Generative reproduction (R)	Vegetative reproduction (R)
1	2.63	2.42	2.78	24	33	18	2	4	21	23	29	30
2	2.73	2.73	2.48	26	26	9	3	14	19	23	22	24
3	0.86	2.82	2.81	30	33	24	3	3	26	25	29	30
4	1.35	2.75	2.56	30	33	8	10	12	28	28	28	29
5	0.55	2.97	2.77	36	35	24	0	12	31	30	30	30
6	1.01	3.12	2.57	31	24	22	2	7	24	24	23	24
7	1.11	2.66	2.37	28	26	8	9	11	25	27	25	26
8	4.67	2.73	2.44	26	23	6	3	17	16	26	14	22
9	2.8	2.74	2.65	21	32	14	3	4	15	16	26	27
10	0.98	3.47	2.75	29	30	22	0	7	26	28	28	29
11	1.06	2.96	2.58	28	27	6	5	17	25	28	26	27
12	1.26	3.01	2.3	31	29	15	3	13	25	27	24	27
13	1.98	1.93	2.56	21	31	0	21	0	20	20	28	28
14	1.29	2.14	1.88	16	24	4	7	5	13	15	21	22
15	0.99	2.32	2.47	27	25	5	3	19	17	25	19	24
16	0.62	2.39	1.48	11	14	0	4	7	9	10	12	13
17	3.14	2.51	2.05	14	23	3	2	9	11	12	19	20
18	1.54	2.14	2.23	12	24	3	1	7	10	12	22	24
19	2.55	2.46	1.77	15	12	3	1	11	12	15	10	12

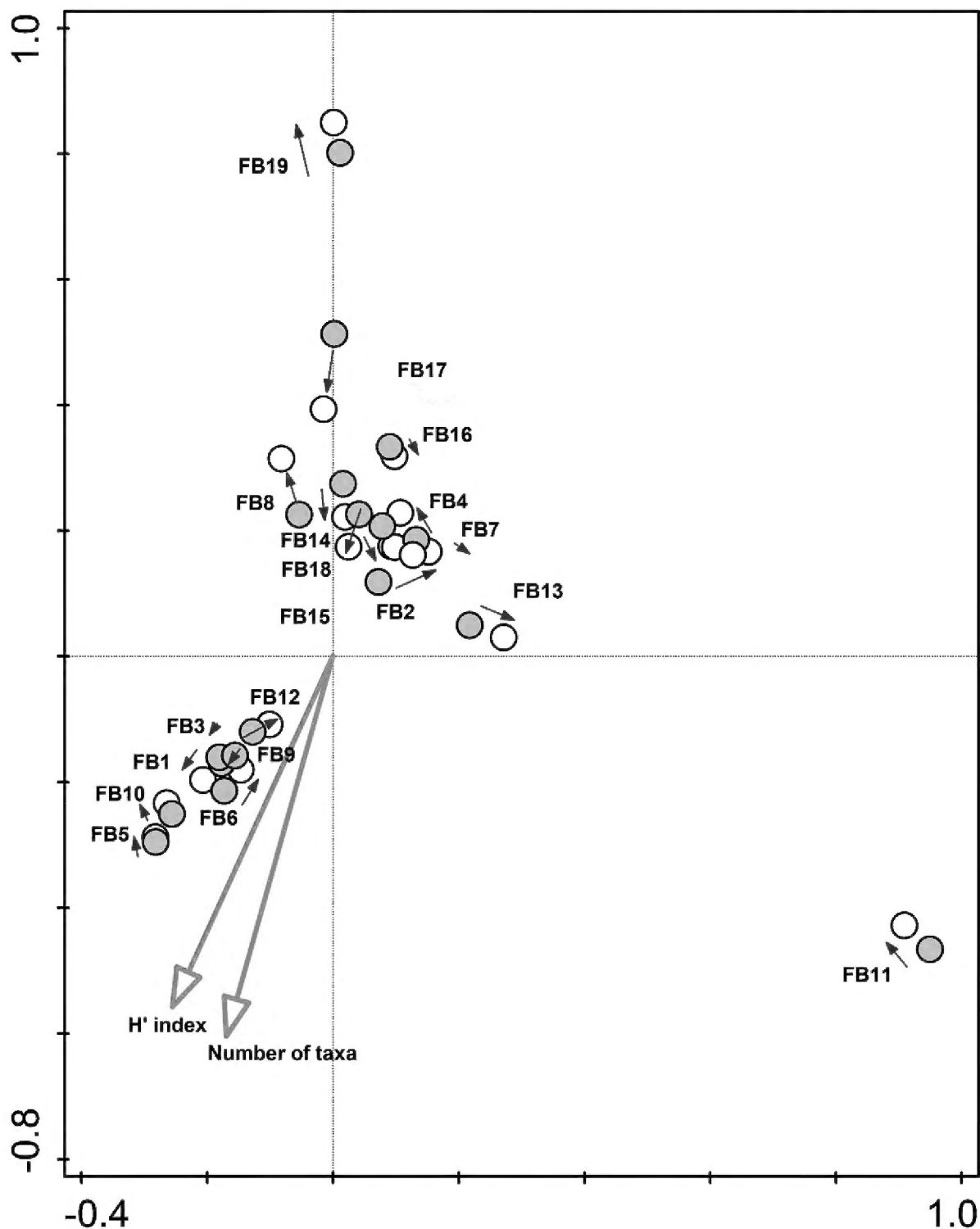


Figure 4. Ordination (CCA) diagram of average change in the studied flowerbeds. Grey symbols represent the initial state of assemblages and white symbols represent the recent state. Distances between the corresponding spots indicate the rate and direction of change.

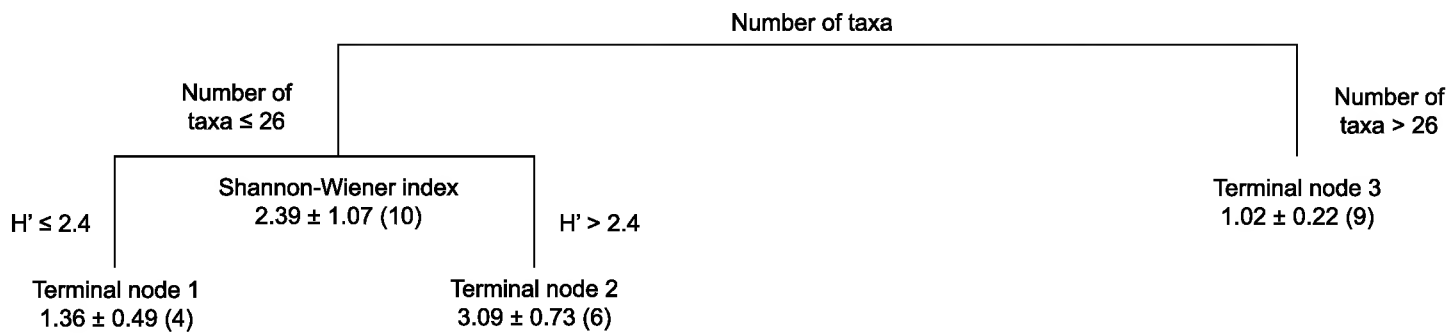


Figure 5. A regression tree showing the effects of number of taxa and Shannon-Wiener index (H'). Mean, standard deviation and number of observations are shown below each node.

Discussion

We found that a high initial number of taxa was related to stability of the assemblage. This is an indication that artificial species-rich assemblages follow similar principles as natural communities (Naeem et al. 1994; Tilman et al. 1996). However, it remains unclear if diversity is the single factor driving this pattern of change in ornamental plantations or whether it can be better explained by environmental factors (climate, precipitation, soil nutrient availability etc.) or the presence of some functional groups (e.g. clonal plants) in an assemblage (Tilman et al. 1997; Hooper and Vitousek 1998). In comparison with processes in natural communities, which are driven by a number of environmental conditions, competition, or stochasticity (Grace and Tilman 1990; Critchley et al. 2002; Kunstler et al. 2012), the garden conditions also include the factor of an initial species pool.

Species diversity at a site affects the establishment and persistence of newly arriving taxa (Tilman and Downing 1994). The stochastic niche assembly theory explains the effects of resource competition and stochastic demography processes on the probability of establishment of new taxa and has been tested in natural and seminatural communities (Tilman 2004). Thus, we expected that more diverse assemblages utilize the limiting resources to a greater degree compared to less diverse assemblages and therefore the fewer unconsumed resources make it harder for new taxa to become established. This assumption is confirmed by the results of the CCA in which both variables (i.e. number of taxa and H' index) are associated with flowerbeds that have a shorter distance between initial and recent times. In addition, we found differences between the identity of a cluster and the initial number of taxa and H' diversity.

Taxa grown in gardens have time to acclimatize to regional conditions in comparison with those introduced via other pathways (Pyšek et al. 2011). In our previous study we assessed the survival of individual ornamental taxa in perennial plantations and we found that 78% of planted taxa can successfully survive over ~10 years (Kutlvašr et al. 2019). In this study we focus on changes in the composition of ornamental assemblages over time. Most of the taxa which did not survive were competitively excluded 1–3 years after planting, and later only few more taxa disappeared. Unfortunately, we do not have comprehensive long-term data for every year since establishment to validate this. However, Hitchmough (2000) noted that for most human-designed plantations, the 3 years following a species' establishment are critical. Taxa that survive this period have better chance to become successfully established. Thus, short-term studies (e.g. Köppler et al. 2014) can show which taxa disappeared but they do not reliably show which taxa are able to become dominant and influence the assemblage by competing with other species.

In our study, certain relationships in the plant community were already obvious following the founding of the flowerbeds. All beds were created using the autoregulation approach; therefore, the effect of interspecific relationships is assumed to sustain the expected abundance of each taxon making the species composition stable and requiring low maintenance. On the other hand, these assemblages are not established for

scientific experiments but mainly for making public spaces attractive. Therefore, the plants need to be charismatic and grow well (Baroš and Martinek 2018). This is the problem relevant to many invasive species where the charisma affects all stages of the invasion continuum, from introduction to eradication (Jaric et al. 2020).

We showed that the stability of assemblages composed mainly of prairie taxa exceeds that of the mixed plantings. This suggests that prairie taxa tend to stabilize the community in our study system. However, Köppler et al. (2014) showed in their comparative study that prairie taxa had lower survival rate compared to steppe taxa. They argued that prairie species are adapted to high precipitation during the main season, whereas the steppes are more tolerant to drought stress during the summer. However, their study only lasted two vegetation seasons and in such short-term experiments, the results may be greatly affected by extremes and fluctuations in environmental conditions (Hitchmough et al. 2004; Pergl et al. 2020). The second problem with short-lasting experiments is that relationships in the community cannot fully establish (Hitchmough 2000).

Our study indicates that garden data can be used for studying the processes of plant invasions and competition. From this and our previous paper on survival and invasive potential of ornamental plants (Kutlvašr et al. 2019) it is obvious, that similar studies on planted alien floras, even established for different purpose, have potential to contribute to understanding ecological processes determining the invasion potential of alien species intentionally introduced to artificial habitats.

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